J Raptor Res. 26(1):13–18

HOME RANGE, HABITAT USE AND BEHAVIOR OF PRAIRIE FALCONS WINTERING IN EAST-CENTRAL COLORADO

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ABSTRACT.—In the two winters 1988–90 we radiotagged 18 Prairie Falcons (*Falco mexicanus*) in east-central Colorado. The home ranges of 10 birds (mostly males), tracked for 17 to 70 d, averaged 30.2 km^2 (minimum convex polygon) and 10.4 km in maximum linear dimension. This home range is far less than reported for the nesting season. Home ranges included significantly more cultivated or fallow land than predicted according to availability. Horned Lark (*Eremophila alpestris*) densities were significantly higher in these habitats than in areas less frequently used by falcons. Larks, almost the exclusive prey of falcons, were attacked in low, high-speed flights, and 13.5% of attacks were successful. Old injuries seen in captured falcons and frequent loss of transmitters from entanglement on barbed wire fences suggest that such attacks are hazardous to falcons. Prairie Falcons were nearly as abundant as Ferruginous Hawks (*Buteo regalis*), and about half as numerous as Rough-legged Hawks (*B. lagopus*). Intraspecific or interspecific aggression was rare compared with reports for Prairie Falcons during the breeding season.

Espacio habitado, uso del hábitat y conducta de halcones de la especie *Falco mexicanus,* invernando en la zona central este de Colorado

EXTRACTO.—Durante 2 inviernos 1988–90 hemos radiocontrolado 18 *Falco mexicanus* en la zona central este de Colorado. El espacio habitado por 10 aves (la mayoría machos), seguidas entre 17 y 70 días, promedió 30.2 km^2 (polígono convexo mínimo) y 10.4 km en dimensión lineal máxima. Esta área habitada es mucho menor que la registrada para la estación reproductora. El área de habitación incluyó significativamente más tierra cultivada o cultivable que lo pronosticado de acuerdo con la disponibilidad. Las densidades de población de las aves de la especie *Eremophila alpestris* fueron significativamente más altas en estos hábitats que en áreas usadas con menos frecuencia por halcones. Las alondras, que son presas casi exclusivas de los halcones, fueron atacadas en vuelos bajos de alta velocidad, y 13.5% de los ataques tuvieron éxito. Halcones capturados con heridas viejas, y la frecuencia en la pérdida de los transmisores, al entramparse en los cercos de alambres de púas, sugieren que tales ataques son azarosos para los halcones. Los *Falco mexicanus* fueron casi tan abundantes como los halcones de la especie *Buteo regalis,* y casi en la mitad del número de los halcones de la especie *Buteo lagopus.* La agresión intraespecie e interespecie fue rara, comparada con los informes que se refieren a los halcones de la especie *Falco mexicanus* durante la estación reproductora.

[Traducción de Eudoxio Paredes-Ruiz]

Falcons in temperate regions seldom have been studied in winter. An exception is the abundant American Kestrel (*Falco sparverius*) which was studied for habitat selection (Koplin 1973, Bohall-Wood and Collopy 1986, Smallwood 1987). This paucity may result from wide dispersal and difficult study logistics when raptors use unpredictable food resources (Newton 1979). Prairie Falcons (*F. mexicanus*), individually marked with holes in remiges, were sighted repeatedly in winter in north-central Colorado. Although the extent of the falcons' movements were estimated, no correlations with habitat types or prey availability were made (Enderson 1964). More recently, telemetry has made a more complete description of movements of wide-ranging falcons feasible.

Band recoveries of Prairie Falcons in winter show dispersal of adult and hatch-year individuals eastward from breeding habitat in the Rocky Mountains and Great Basin to the Great Plains. We determined the size of winter home ranges, territoriality, and habitat use on the Plains where previous roadside counts had shown Prairie Falcons to be the second or third most abundant winter raptor (Enderson

1965, Johnson and Enderson 1972, Bauer 1982). We predicted that habitat use by Prairie Falcons would be correlated with prey abundance and distribution.

STUDY AREA

This study was conducted about 48 km east of the Rocky Mountains near Ellicott, Colorado. The area has gentle drainages with no permanent streams. Elevation varies between 1700–2070 m. Short-grass prairie was most prevalent and was dominated by Blue Grama (*Bouteloua gracilis*). Sand Sage (*Artemisia filifolia*) prevailed on sand hills. Overgrazing has resulted in abundant Yucca (*Yucca glauca*), Bushy Buckwheat (*Eriogonum effusum*), and Snakeweed (*Gutierrezia sarothrae*) dispersed among Blue Grama, the latter often grazed shorter than 3 cm. Cultivated areas included Winter-wheat (*Triticum anetivum*), Milo (*Sorghum* sp.) and sod farms. Because rainfall averaged only 32 cm annually, much cultivated land was fallow and was dominated by open stands of Common Sunflower (*Helianthus annuus*), Russian Thistle (*Salsola australis*), Sweetclover (*Melilotus* sp.), and Tansy-aster (*Machaeranthera* sp.). Horned Larks (*Eremophila alpestris*) were ubiquitous and the only conspicuous small passerine.

METHODS

Prairie Falcons were captured with noose-harnesses on Rock Doves (*Columba livia*) or bal-chatri traps (Berger and Mueller 1959) in November–February 1988–90. Each falcon was fitted with a 216-mHz transmitter weighing 15 g, sewn with nylon dental floss to the two central rectrices. Battery life was about 3 mo. Tracking was by hand-held yagi antennas, using aircraft when signals could not be obtained from the ground. When possible, falcons were approached until they could be seen with a spotting scope. Triangulation was used when the bird could not be seen. Generally, we sought to relocate each bird every 3 or 4 d unless a signal could not be found after repeated searches. This interval was chosen to provide individuals time to move between observations, thus reducing the possibility that the position on one observation would influence strongly the position on a second observation. We tracked mainly in mornings, expending about 430 hr. Three falcons were followed from sunrise to sunset on four separate days to check daily movement. Winter range was determined by minimum convex polygon technique (Mohr 1947) because observations were scattered and not arranged linearly. Ranges were plotted on vegetation maps, and the areas of four cultivated vegetational types, and of rangeland were totalled for each bird.

The number and location of Horned Larks were recorded in winter 1989–90 along a 124 km route including all vegetation types. Counts were made on 12 d in a 6-wk period and larks within 300 m of the road were counted after flocks flushed. To speed the counting before the flock disappeared, each flock was assigned one of the following size categories: 1–12, 13–24, 25–36, 37–50, 51–65, and >65. However, in our analysis of abundance we assigned each flock an index value of 6, 18, 30, 44, 58, or 100 individuals, respectively. We used an abundance index instead of analysis on a per flock basis because observations suggested that flock sizes are not fixed and may be variable by habitat and through time. Aerial photos, augmented by observations in the field, were used to create a vegetation map specific to the 124 km route. The position and index value of each flock of larks was entered on the map.

Prairie Falcon locations and abundance index values for Horned Larks were categorized by vegetation type and compared using chi-square analysis of use compared to habitat availability. Simultaneous analysis of habitat use was used to determine habitat preference or avoidance (Neu et al. 1974).

RESULTS

We caught and radiotagged 17 males and 1 female Prairie Falcon; 11 were caught in 1988–89 and seven in 1989–90 (Table 1). One bird was given a second transmitter after the first was lost. All sightings, including first encounters with falcons that were given radios, included 57 males, 18 females, and 33 not identified as to sex.

Locations of 10 falcons tracked at least seven times during periods from 17–70 d were included in the analysis. Fewer locations or days apparently biased home-range estimation downwards (Table 1). The remaining eight tagged birds, including five hatch-year males, could be found for 10 d or fewer after tagging. We suspect they either moved far from the area or lost their transmitters. With one exception, these eight falcons showed small range areas in the brief periods they were tracked.

In all, we found six functioning transmitters on the ground near barbed-wire fences, five of which were still attached to tail feathers. The tips of the antennas were tightly coiled suggesting they were struck as the bird barely cleared the top wire in their characteristic high-speed, low-level attacks on prey. One transmitter was attached to the top wire of a fence. None were found below fence posts, suggesting that radios were lost due to collision. We saw two Prairie Falcons with missing central feathers near the capture sites, but could not be sure they were previously tagged.

Foraging Ranges and Habitat Use. Minimum home ranges, the area enclosed when outermost points are connected to form a polygon, averaged 30 km^2 (range 12.3–68.0) after one range of 583 km^2 for an adult male was excluded (Table 1). The average maximum linear dimension for the nine ranges was 10.4 km (range 5.8–17.8) excluding one 42 km measurement.

Table 1. Prairie Falcons radiotagged in El Paso County, Colorado, during winters 1988–90. Measurements are rounded to nearest unit.

AGE,[a] SEX	CAPTURE DATE	NO. DAYS OBSERVED	LOCATIONS RECORDED	RANGE AREA (km^2)	LONGEST AXIS (km)
AM	9 Dec 1989	1	1	—	—
IM	16 Dec 1989	1	1	—	—
IM	13 Dec 1989	2	2	—	1
IM	3 Dec 1988	5	3	3	4
IM	1 Jan 1989	4	3	5	4
AM	10 Dec 1988	7	5	14	6
IM	12 Jan 1989	8	6	1	2
AM	10 Jan 1989	10	7	6	5
AM	4 Feb 1989	27	7	22	10
AM	3 Jan 1989	17	8	68	18
AF	25 Nov 1989	70	8	12	6
IM	21 Jan 1989	32	12	22	11
IM	16 Dec 1989	36	14	33	9
AM	1 Jan 1989	55	14	34	12
AM	15 Jan 1989	54	17	27	9
IM	18 Jan 1990	61	19	16	8
IM	30 Dec 1988	41	20	38	11
AM	21 Jan 1990	40	22	583	42
Means (± Standard Error)[b]			—	30.2 ± 5.5	10.4 ± 3.8

[a] A = Adult; I = Hatch year.

[b] Excluding adult male captured 21 January 1990 and individuals observed for fewer than 17 d.

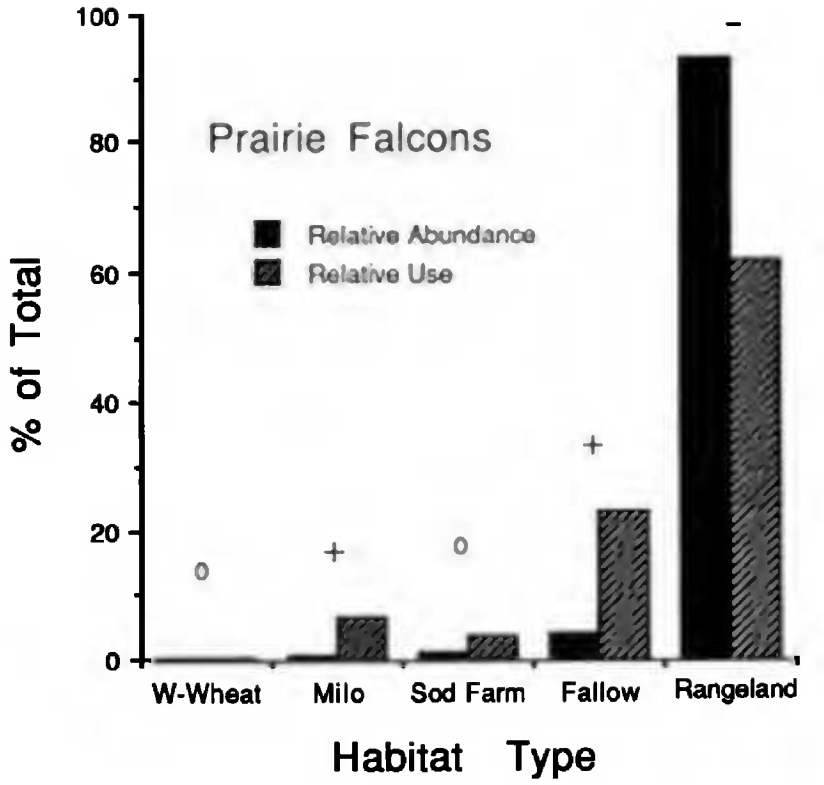
Each of 141 locations for the 10 Prairie Falcons was categorized by vegetation type. This observed habitat use was compared to expected habitat use based on habitat availability. We rejected the null hypothesis that falcons frequented habitat in proportion to its availability ($\chi^2 = 139.8$, df = 4, $P < 0.001$). Simultaneous analysis of habitat use revealed that falcons frequented milo fields and fallow land significantly more than expected ($P < 0.05$; Fig. 1). Rangeland was used significantly less than expected ($P < 0.05$).

Two falcons were followed from sunrise to sunset one day each, and another for two non-consecutive days. On all four occasions the birds were most sedentary in midday. Two falcons flew over a path about 10 km long, and one, whose range was 42 km in maximum dimension (Table 1), flew about 55 km on each of the two days he was followed. This bird was one of two adult males that visited the only rock outcrops in the study area used by nesting Prairie Falcons in recent decades.

Interactions with Prey. Prairie Falcons attacked prey 40 times and all but 3 attacks involved Horned Larks. Other prey included two mice (Cricetidae), and a Western Meadowlark (*Sturnella neglecta*). Of the 40 attacks, 6 were successful, resulting in the capture of 5 larks and 1 vole (*Microtus* sp.).

Larks seemed attracted to roadsides, perhaps because of taller and more diverse vegetation, enhancing our counts. Larger flocks were encountered more often in the few days when snow cover was complete. Most Horned Larks occurred in larger flocks rather than small ones. In the 12 lark censuses, 236, 93, 61, 29, 80 and 48 flocks were observed with 1–12, 13–24, 25–36, 37–50, 51–65 and >65 larks, respectively. Although fewer large flocks were seen, these flocks were subject to the majority of falcon attacks. Of attacks on larks by Prairie Falcons, 24 (65%) were at flocks exceeding 50 individuals (23% of all flocks).

Frequencies of vegetation types along the route used to count larks were similar to those in falcon winter ranges, with rangeland predominating (Fig. 1). We rejected the null hypothesis that larks inhabited vegetation types in relation to vegetation frequency ($\chi^2 = 485.5$, df = 4, $P < 0.001$). Simultaneous analysis of habitat use revealed that Horned Larks used all cultivated habitats significantly more



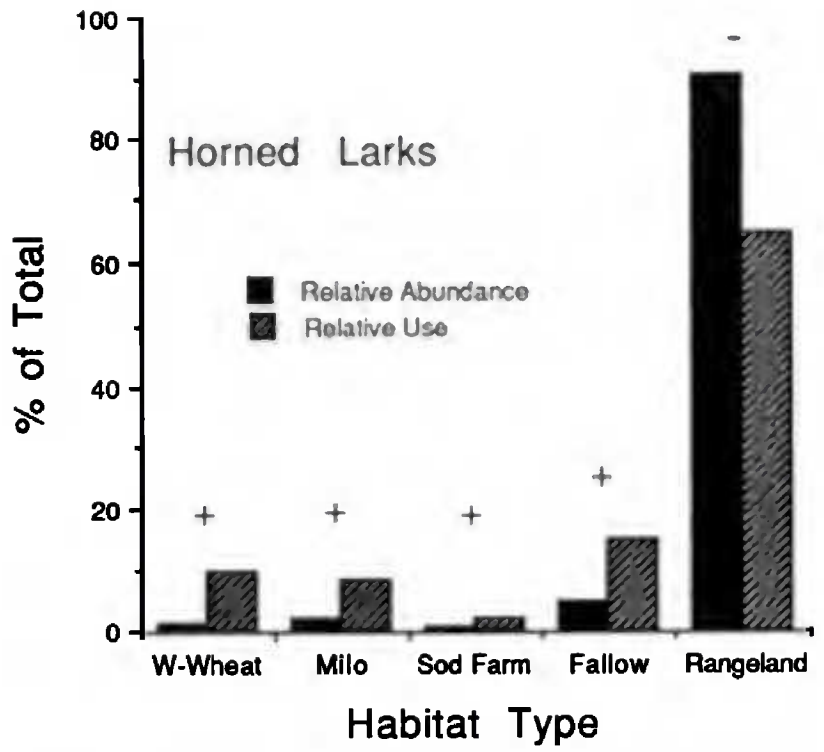


Figure 1. Habitat use by Prairie Falcons and Horned Larks. Symbols above the bars indicate selection: + = greater use than expected, − = less use ($P < 0.05$) and 0 = no difference.

than expected ($P < 0.05$) and frequented rangeland significantly less than expected ($P < 0.05$). Furthermore, 39% of all lark flocks over 50 individuals were found in cultivated fields comprising only about 10% of the total habitat.

Aggression and the Abundance of Other Raptors. Rough-legged Hawks (*B. lagopus*) were the most common raptors and were twice as abundant as Prairie Falcons (Table 2). Ferruginous Hawks (*Buteo regalis*), Golden Eagles (*Aquila chrysaetos*), and Northern Harriers (*Circus cyaneus*) were also common. Fence posts, electric distribution and transmission line poles were numerous and the latter have been shown to increase the local density of raptors on this study area (Stahlecker 1978).

Table 2. Raptors seen in El Paso County, Colorado, during 28 d, November–February 1989–90. All roadside counts were made before noon on calm days. Total distance traveled = 2051 km.

SPECIES[a]	km/INDIVIDUAL
Rough-legged Hawk	22
Ferruginous Hawk	51
Prairie Falcon	54
Golden Eagle	73
Northern Harrier	171
American Kestrel	228
Merlin	256

[a] Bald Eagles (*Haliaeetus leucocephalus*) were seen three times and Red-tailed Hawks were seen two times; 59 raptors were too distant to identify.

Prairie Falcons interacted with conspecifics only once, when an adult male flew about 1 km to make a shallow dive at another, probably a male. The former landed on a fence post when the other flew slowly away. Several times we saw falcons perched within a few hundred meters of each other without aggression. Overlap between winter ranges determined by telemetry was insignificant, but we observed the ranges of adjacent birds for only a few weeks.

Interspecific aggression was seen rarely, although other raptors were common. Rough-legged Hawks were attacked three times by falcons after we had released Rock Doves as bait in the immediate vicinity. Common Ravens (*Corvus corax*) were chased twice under similar circumstances. Perched falcons were the subjects of shallow stoops to within 1 m by a Merlin (*Falco columbarius*), a Northern Harrier, and a Rough-legged Hawk. The falcons did not fly.

DISCUSSION

Most field studies of raptors in winter were in modified and structurally variable habitats which created irregular distributions of both raptors and prey. In southeastern Idaho, where cultivated farmland and rangeland were interspersed, Rough-legged Hawks preferred the former where voles were abundant. Golden Eagles preferred rangeland where

Black-tailed Jackrabbits (*Lepus californicus*) were available (Craig et al. 1986). Preston (1990) found that Red-tailed Hawks (*Buteo jamaicensis*) and Northern Harriers were distributed nonrandomly in central Arkansas in winter; harriers responded to prey abundance and cover density, and the hawks to prey abundance and perch availability. Patches of vegetation highest in prey, but with deep cover, were used by both species less frequently than predicted. Male and female American Kestrels wintering in Florida defended territories in different habitats (Bohall-Wood and Collopy 1986); males used closed habitats that seemingly restricted access to insect prey compared to females in more open areas (Smallwood 1987). In the winters 1960–62 Prairie Falcons in Colorado fed primarily on Horned Larks, but habitat was uniformly winter-wheat and no test of habitat was attempted (Enderson 1964).

Of the 18 Prairie Falcons we radiotagged in this study, 8 could not be tracked for long, mainly because transmitters failed or fell off after the birds collided with fences. Transmitter failure probably contributed to an underestimate of the time wintering falcons actually remained on the study area. Some of the falcons we saw or captured were probably transient and failed to remain and establish a winter range. In 1960–62, nine Prairie Falcons, wing-marked mostly in November in a winter-wheat area of north-central Colorado, remained an average of 67 d (range 20–117; Enderson 1964) compared to 43 d (17–70) in the present study. Of the eight falcons we were able to track only briefly, five were radiotagged on 16 December or earlier.

Cultivated areas, including fallow land, attracted Horned Larks, which in turn probably attracted Prairie Falcons that fed on them. Larks may be able to locate more food, including weed seeds, in such areas. Increased cover associated with fallow fields may also lower wind and enhance shelter compared to the open prairie community. On the other hand, cover provided by Milo fields and fallow land may have concealed falcons attacking the high concentrations of larks found there.

The relationship between lark and Prairie Falcon habitat use was not perfect. Horned Larks used wheat and sod areas more than predicted, but falcons seemed to show no preference. Larks are easily seen on sod and wheat; we may have overestimated their abundances there compared to other types.

We believe Prairie Falcons oriented to the larger flocks of larks, exposed while moving in short flights as the larks fed. Although Kenward (1978) showed a Goshawk (*Accipiter gentilis*) was less successful attacking larger flocks of Wood Pigeons (*Columba palumbus*), Prairie Falcons did not seem distracted by many, panicked Horned Larks. Prairie Falcons that found concentrations of larks did not move far and sometimes sat for several hours unless flushed by automobiles. Once falcons discovered dense concentrations of Horned Larks, they remained in the area.

We discounted perch availability as a factor in winter range size. Poles of various types are abundant at borders of rangeland pastures and cultivated areas alike, and such areas are small compared to the size of a falcon's range. Although many rangeland areas have few fences, power poles were always present.

The average home range in this study was 30.2 km^2 for nine Prairie Falcons (Table 1). In the nesting period in southern Idaho, 18 adult Prairie Falcons used an average range of 107 km^2 (Dunstan et al. 1978). In the Mohave Desert, Harmata et al. (1978) found mean home range size during nesting was 72 km^2 for males ($N = 3$) and 47 for females ($N = 3$). The average maximum dimension of range in this study was 10.4 km excluding that of one wandering adult male, and was 8.8 km for 11 marked Prairie Falcons in north-central Colorado in the winter of 1960–61 (Enderson 1964). These values were unexpectedly small considering these falcons can fly 10 km in less than 7 min.

The two largest ranges we measured were of adult males that were not associated with cultivated habitats. One of these birds was in a region that was entirely rangeland. The other traveled so widely, he probably encountered cultivated areas and Horned Lark concentrations but did not exploit them for long. Both males visited potential nest cliffs in their long flights.

Where there was no cultivated land, Prairie Falcons have been more sparsely distributed. In southeastern Colorado, one Prairie Falcon was seen per 200 km driven in prairie habitat in a 3400 km roadside survey during the winters of 1983–88 (Andersen and Rongstad 1989), compared to one individual per 54 km in this study.

We cannot fully explain the unequal sex ratio of falcons (1 female : 3.2 males) seen in this study. Sex is generally easy to determine in this species and individuals not identifiable were usually far away. Prey larger than larks were rare, a factor that may

have tended to exclude female falcons. Larks may be too small for females to exploit regularly. Prairie Falcons were found in a ratio of 1:0.6 in winter in northern Colorado wheat country where larger passerines and Ringed-necked Pheasants (*Phasianus colchicus*) were common (Enderson 1964).

Only 5 in 37 (13.5%) attacks on Horned Larks were successful. Larks weigh about 9% the body weight of a male Prairie Falcon and appeared vastly more maneuverable in flight. High-speed attacks low to the ground result in surprise and none of the misses we saw were followed by second attempts. We caught three males with substantial old wounds on a patagium, foot, or cere, suggesting attacks in fenced country are hazardous. Frequent loss of transmitters at fences underscores the risk.

Roalkvam (1985) summarized 13 reports on the hunting effectiveness of Peregrine Falcons (*Falco peregrinus*) outside the breeding season and found a mean success rate of 12.7%. Buchanan et al. (1986) found a 14.6% success rate for peregrine first-attempts on Dunlins (*Calidris alpina*). Prairie Falcons ate mainly Horned Larks in this study, a sharp contrast to their varied diet in the breeding season. In an extreme case 39 species of reptiles, birds, and mammals were used by 19 pairs in the Mohave Desert (Boyce 1985).

Aggression among Prairie Falcons was not seen and winter territories, as described in American Kestrels (Smallwood 1987), seem unlikely. Prairie Falcons were conspicuously passive given the almost continual presence of hawks or other falcons. In the nesting season, Prairie Falcons are perhaps more aggressive. Dunstan et al. (1978) recorded 10 intraspecific and 5 interspecific aggressive encounters while following radio-tagged nesting adults.

ACKNOWLEDGMENTS

C. Hecock, S. Kempers, and M. Robert provided assistance with the field work. A. Harmata, I. Newton and C.M. White made valuable comments on the manuscript, and J. Newberry helped with its revision.

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Received 27 August 1991; accepted 15 November 1991